

# Ecological parameters of the Northern Brown Snake, *Storeria dekayi*

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**ABSTRACT** — Data were gathered on 702 Northern Brown Snakes, *Storeria dekayi*, captured 1,041 times at two similar sites in Lancaster County, Pennsylvania, USA, during the years 1960–1967. Eight-nine percent of the captures were of active snakes. The overall population size was estimated to be 1,095 (S.E. 201) individuals, and the density varied between 66 snakes/ha and 300 snakes/ha at the two sites. Total biomass at the two sites was over 2.5 kg (860 g/ha). The combined population was composed of 188 juveniles (including neonates) and 512 adults, a juvenile to adult ratio of 0.37:1.00 and an adult male to female sex ratio of 0.81:1.00. Both ratios were statistically significant ( $P = 0.05$ ). The snakes were active for an average of 200 days each year between April and October. The annual cycle was bimodal with most activity in the spring and early summer and a lesser peak of activity in the early fall. Daily activity was also bimodal in summer, with most activity in the morning and a second spike in activity in late afternoon and early evening. Active snakes had body temperatures of 10.0–29.5°C. Additional data and comparisons between the two sites are reported on population dynamics, activity periods and hibernation, thermal ecology, habitat, movements, reproduction, feeding behaviour, and injuries, predation and ectoparasites.

**T**HE Northern Brown Snake, *Storeria dekayi*, ranges in North America from southern Maine, Quebec and Ontario west to Wisconsin, Minnesota, and the eastern Dakotas, and south through Florida in the East, to the Gulf of Mexico in the Midwest (Christman, 1982; Ernst & Ernst, 2003). Although widespread and not uncommon, its behaviour and ecology have not been adequately studied. Freedman & Catling (1978, 1979) and Catling & Freedman (1980) reported on the movements and population dynamics of an Ontario, Canada population, and Clausen (1936), Kofron (1979) and Trapido (1940) reported on reproductive aspects of the species, but most available data are of an anecdotal nature (see Ernst & Ernst, 2003 for a summary).

The Northern Brown Snake, *Storeria dekayi*, was studied in Lancaster County, Pennsylvania, USA from March 1960 through July 1967. It was hoped that specific data from this study would fill in many of the gaps our knowledge of this snake, and to present comparative material with studies on it conducted elsewhere. Data from the study of *S. dekayi* are presented below.

## METHODS

### Study Areas

Data were gathered on two disjunct populations of *S. dekayi dekayi* located about 4 km apart in Lancaster County, Pennsylvania, USA. Site 1 (Edward Hand) contained the largest population, and was located on a 2 ha abandoned 'shanty town' behind the playing fields of Edward Hand Junior High School near the southeastern corner of the city of Lancaster. The site was in an open mesic woodland dominated by oak (*Quercus* sp.), maple (*Acer* sp.), and locust (*Robina* sp.) trees bounded on the south by a gravel road, the Conestoga Creek to the north, a row of houses and an open field to the west, and an Army Reserve facility on the east. Much debris remained from the destruction of the shanties in 1959 in the form of sheets of tin, tar paper, wooden boards, and other discarded human trash, as well as some logs, which provided excellent ground cover for snakes. The tree canopy was relatively open, but all sections of the site were shaded at sometime during the day. A drainage gully, fed by a natural spring, ran northward through the western third of the site.

The second study site (Slackwater) was along an approximately 100 m loosely constructed, north-south, stone fence on a wooded hill at Slackwater, approximately 1 km south of Millersville, Pennsylvania. It overlooked and sloped into the Conestoga Creek to the south through an open mesic woodland dominated by oak (*Quercus* sp.), maple (*Acer* sp.), and tulip poplar (*Liriodendron* sp.) trees, and was bounded by a pasture to the north. The total area of the site was about 1.5 ha.

The bedrock at both sites was composed predominately of limestone, and the overall characteristics of the two Pennsylvania sites agreed closely with those of other study sites of *S. dekayi* in Kansas (Fitch, 1999), in North Carolina (Palmer & Braswell, 1995), and in Ontario (Catling & Freedman, 1980).

### Procedures

Snakes were hand collected. Each snake was marked by scale clipping (Blanchard & Finster, 1933; Fitch, 1949). At each capture, the total body length (TBL), snout-vent length (SVL), and tail length (TL) were recorded with a metal metric tape measure accurate to 1.0 mm, and the snake was weighed with a spring scale accurate to 0.1 g. Each snake was sexed (Conant & Collins, 1998; Palmer & Braswell, 1995). The following data were also recorded: date, time, type of activity (snakes were considered active if responsive to disturbance; dormant, if not responsive), air temperature (AT), surface temperature (ST), cloacal temperature (BT), presence or absence of a food bolus, and any signs of injury or parasites. BT was taken with a quick reading Schultheis cloacal thermometer, and AT and ST were recorded with the unshaded bulb of a standard laboratory mercury thermometer. Snakes swollen with a food bolus were gently palpated to force regurgitation of the ingested prey. These prey and others from natural observations of feeding were recorded.

The statistical methods used to analyse data were taken from Sokal & Rohlf (1973). The acceptable confidence level for all statistics was set at 0.05.

### RESULTS

A total of 702 *S. dekayi* were marked (Edward Hand, 603; Slackwater, 99), and captured 1,041 times (Edward Hand, 855; Slackwater, 186). Of the 1,041 captures, 935 (89.8%) were of active snakes (Edward Hand, 785, 91.8%; Slackwater, 150, 80.7%), and 106 (10.2%) were considered dormant (Edward Hand, 70, 8.2%; Slackwater, 36, 19.3%). All captures were at ground level of exposed or under cover snakes; no *S. dekayi* was found above ground level, similar to what was reported elsewhere (Neill, 1948).

#### Annual Activity Period

Responsive *S. dekayi* were found, either under shelters or surface active, from 28<sup>th</sup> March to 1<sup>st</sup> November, an average annual activity period of about 200 days, and a maximum one of 219 days (Edward Hand 28<sup>th</sup> March – 1<sup>st</sup> November, 219 days; Slackwater 16<sup>th</sup> April – 13<sup>th</sup> October, 181 days). The snakes had slightly varying annual active periods during 1961–1966; with the greatest number of active days at both sites occurring in 1962, and the fewest numbers of active days at both sites in the drought year 1966 (Edward Hand, 189 days; Slackwater 175 days). Both the maximum and minimum active days for the six complete years of study, 1961–1966, at the two sites were significantly different (Chi square test, 12.029, 5 df,  $P = 0.05$ ).

The annual activity period was bimodal (Tables 1 and 2), with a spring peak period from 20<sup>th</sup> April – 25<sup>th</sup> June when 555 (59%) of the total 935 captures were made, and a lesser activity period in the fall from 3<sup>rd</sup> September – 20<sup>th</sup> October when 244 (26%) captures occurred. Early spring Pennsylvania records (28<sup>th</sup> March – 30<sup>th</sup> April) represented for the most part individuals that had emerged from hibernation, but had not dispersed from their communal hibernaculum. The late September and October records were mostly of individuals aggregated at hibernacula.

#### Daily Activity Period

The timing of daily activity varied with the season at both sites (Table 2). Although most captures were of individuals under cover, some *S. dekayi*

Month	Adult Males	Adult Females	Juveniles	Totals
M	3	0	0	3
A	49	41	43	133
M	130	78	49	257
J	58	88	30	176
J	24	32	9	65
A	21	30	1	52
S	38	35	16	89
O	65	51	39	155
N	2	3	0	5
Totals	390	358	187	935

Table 1. Frequency of captures by age category and sex of active *Storeria dekayi* by months (1960–1967).

were found basking or moving over the surface of the ground. From April to early June and in September and October, some snakes were found moving or basking in late morning or early afternoon (10:00–15:30 hrs). Daytime surface activity slowed or ceased from mid-June through August, when the snakes became either vesper time (two records at 19:45 and 20:13 hrs) or nocturnal (based on the absence of *S. dekayi* under selected shelters in the evening, but their presence there at 07:00–08:30 hrs the next morning). Three individuals were found moving in the early night (21:17, 22:48, 22:55 hrs), and another was discovered eating an earthworm at 20:48 hrs. Possibly, most summer activity occurs between 20:00 and 24:00 hrs).

#### Thermal ecology

Body and environmental temperatures were recorded during 815 captures of adult *S. dekayi* (juveniles and neonates were too small to measure); 725 (77.5%) captures of active snakes, 90 (84.9%) of inactive individuals. Mean BT of active adult snakes was 25.3°C (10.0–29.5°C). Seventy percent ( $n = 508$ ) of the active snakes had BTs in the 20–27°C range; the most frequent BTs of active snakes were 23° ( $n = 152$ ), 24° ( $n = 103$ ), and 22°C ( $n = 90$ ). At Edward Hand, the range of BTs of active *S. dekayi* was 10–27.5°C (mean

24.9°); at Slackwater, active snakes had BTs of 11.2–27.0°C (mean 25.8°). No statistical difference occurred between the BTs of the snakes at the two sites (Chi square, 89.245, 50 df, n.s.) Overall, active snakes had a mean body temperature differential of 1.8°C compared to AT, and a mean 0.8°C differential to the ST (Table 3 gives the cloacal and environmental temperatures by activity).

Inactive snakes were all considered to be hibernating or to be entering hibernation. The lowest BT (3°C) of inactive *S. dekayi* were of five adults hibernating in a ball in the stone wall at Slackwater on 20<sup>th</sup> January 1967; the lowest BT 3.5°C of an inactive snake at Edward Hand was of a hibernating adult within a log on 10<sup>th</sup> January 1963. The highest BT (7°C) for inactive snakes was recorded from five adults balled together in a shallow depression under tarpaper at Edward Hand on 31<sup>st</sup> March 1963, and from an adult in the stone wall at Slackwater on 12<sup>th</sup> December 1966. Inactive snakes at Edward Hand ( $n = 15$ ) had BTs of 3–7°C (mean 4.3°C); at Slackwater inactive adults ( $n = 30$ ) had the same range in BTs, but averaged only 4°C. Overall, inactive snakes had a –1.2°C BT differential with the AT, and a 0.2°C differential with the ST.

#### Population dynamics

A combined total of 702 individual *S. dekayi* were captured and marked at the two sites during 1960–1967 (see above). Only 42 (4%) captures were of exposed *S. dekayi*; 999 (96%) captures were of snakes hiding under some shelter. Exclusive of hibernating aggregations, as many as six active individuals were found sharing the same shelter at Edward Hand, but never more than one active *S. dekayi* was found under a shelter at Slackwater. Daily study duration was equal at the two sites; about 4 hours per day. The number of captured individuals per day averaged 10.8 (0–30) at Edward Hand, but only 2.8 (0–11) per day at Slackwater. The overall proportion of recaptures of marked snakes (as well as those of each of the

Time (hrs)	M	A	M	J	J	A	S	O	N	Totals
07:00	0	0	3	4	1	2	2	0	0	12
08:00	0	0	19	15	1	1	2	0	0	38
09:00	0	18	23	18	3	0	1	1	1	65
10:00	0	12	31	28	2	0	2	11	4	90
11:00	1	14	29	22	2	0	16	25	0	109
12:00	1	18	28	19	3	0	14	23	0	106
13:00	1	21	38	18	0	0	15	31	0	124
14:00	0	18	31	20	0	0	14	15	0	98
15:00	0	11	29	12	5	1	10	14	0	82
16:00	0	14	17	9	8	10	8	10	0	76
17:00	0	3	6	4	11	12	4	16	0	56
18:00	0	4	3	2	10	10	1	9	0	39
19:00	0	0	0	2	7	5	0	0	0	14
20:00	0	0	0	3	11	3	0	0	0	17
21:00	0	0	0	0	1	2	0	0	0	3
22:00	0	0	0	0	0	6	0	0	0	6
<b>Totals</b>	<b>3</b>	<b>133</b>	<b>257</b>	<b>176</b>	<b>65</b>	<b>52</b>	<b>89</b>	<b>155</b>	<b>5</b>	<b>935</b>

two sites) did not increase as more individuals were marked (Spearman's coefficient of rank correlation,  $r_s = 0.439$ ,  $P > 0.05$ ). Only 104 (14.8%) of the marked snakes were recaptured more than once; one male was recaptured six times, and four females were recaptured five times each.

The interval between recaptures gives a rough estimate of survivorship. Six *S. dekayi* first marked as juveniles averaged 4.2 years (1–7 years) between first and last capture. The male mentioned above was captured six times in 5 years, and the four females captured five times each averaged 3.7 years (2–7 years) between their first and last capture.

The population size for both sites combined and those of the two individual sites were calculated with the weighted least squares method of Schumacher & Eschmeyer (1943), recommended by Turner (1977). This method has the advantage of eliminating bias caused by unequal recapture rates, as it is based on a series of collecting periods rather than only on two, as in the Peterson Estimate (Begon, 1979). Data from a series composed of the last 300 collections of *S. dekayi*

**Table 2.** Frequency of capture of active *Storeria dekayi* by months and hours (1960–1967).

between 1964 and 1967 were used to calculate the population sizes, and the population size limits were determined by adding and subtracting two standard errors (S.E.; 95% confidence level) from the population sizes (Schumacher & Eschmeyer, 1943). The overall population size was estimated to be 1,095 (S.E. 201) *S. dekayi* with a possible range of 693–1,497 individuals. The Edward Hand population was estimated to contain 704 (S.E. 108) individuals (range of 488–920); the Slackwater population was only estimated to be composed of 152 individuals (S.E. 48; range 56–248). Population density was estimated to be 66/ha at Slackwater, and 300/ha at Edward Hand. Most Slackwater captures were made at the stone wall, but the *S. dekayi* at Edward Hand were more scattered among the surface debris.

Snakes were weighed during 904 of the 1,041 total captures at the two study sites. Adult males (304 captures) had a mean mass of 3.00 (1.85–3.55) g, adult females (388 captures) had a

Activity	Body Temperature	Air Temperature	Surface Temperature
Hibernate ( $n = 90$ )	4.2 (3.0-7.0)	4.0 (-1.0-7.0)	6.2 (2.0-10.0)
Under shelter (active) ( $n = 683$ )	23.0 (10.0-26.0)	24.0 (8.0-36.0)	21.0 (10.0-26.0)
Basking ( $n = 6$ )	28.5 (26.0-29.5)	29.1 (25.0-32.0)	26.8 (24.3-30.5)
Moving ( $n = 21$ )	25.5 (24.0-28.2)	27.5 (25.3-30.0)	25.09 (22.5-27.5)
Feeding ( $n = 5$ )	24.2 (22.0-26.5)	26.2 (25.0-28.0)	24.8 (22.0-28.0)
Mating ( $n = 10$ )	21.6 (20.0-23.0)	24.6 (22.0-26.0)	22.2 (20.0-24.0)

**Table 3.** Mean body and environmental temperatures and ranges (°C) of *Storeria dekayi* by activities.

mean mass of 3.85 (1.88–4.43) g, and juveniles (212 captures, including neonates) averaged 0.82 (0.20–2.21) g. Total biomass at the two sites was 2579.64 g, a biomass density of 859.88 g/ha. At Edward Hand, weights were taken during 728 of the 855 captures, and yielded a total biomass of 1974.16 g, and a biomass density of 987 g/ha. At Slackwater weights taken during 176 of 186 captures yielded a total biomass of 605.48 g and a biomass density of 403.6 g/ha.

Male *S. dekayi* were considered mature at 19.0 cm SVL or larger, and females at 22.0 cm SVL or larger (Ernst & Ernst, 2003). The combined population was composed of 188 juveniles and 512 adults, a ratio of 0.37:1.00. The overall adult male to adult female ratio was 0.82:1.00. Both of these ratios are significantly different from 1:1 (Chi square test, 4.100, 1 df,  $P = 0.05$ ). At Edward Hand, the adult sex ratio was 0.90:1.00, and the juvenile to adult ratio was 0.44:1.00; at Slackwater these ratios were 0.52:1.00 and 0.03:1.00, respectively. The juvenile to adult ratios at both sites and the adult sex ratio at Slackwater were significantly different from 1:1 (Chi square test, 5.09, 1 df,  $P = 0.05$ ).

#### Movements

Because relatively few recaptures were made of individual *S. dekayi*, home ranges were calculated using the circular method (Fitch, 1999). The average home range diameter of snakes that had

moved and were captured more than twice at both sites was 47 m (28–64 m,  $n = 41$ ) for males, and 39 m (22–54 m,  $n = 63$ ) for females. Most recaptures were made less than 40 m from the previous capture site (73% of males, 90% of females). Ten gravid females were recaptured at their original capture site. Home ranges at Slackwater were smaller, probably due to less available suitable habitat; 46 m (25–54 m) for males, 38 m (22–45 m) for females. At Edward Hand, males had average home ranges of 51 m (28–64 m), and females 41 m (25–54 m). The greatest distances moved between captures occurred at Edward Hand: 670 m and 555 m by two males with 30.5 cm, and 31.8 cm SVLs, respectively, and 604 m by a 38.1 cm SVL female. All three of these snakes were only recaptured once.

#### Reproduction

Observations on reproduction of wild *S. dekayi* were limited. However, 16 adult males (SVL 19.0–22.2 cm) and 16 adult females (SVL 22.0–40.2 cm) were brought into the laboratory and housed in mixed sex pairs, and some data were obtained from them. Captive copulatory behaviour occurred from 20<sup>th</sup> April to 15<sup>th</sup> May.

Males apparently find females by following female pheromone trails (Ernst & Barbour, 1989). Courtship behaviour by the Pennsylvania males consisted of rubbing the chin along the female's back and neck and performing a series of caudocephalic waves while laying in contact

Age (years)		SVL (cm)	N	Mass (g)	N
Neonate		7.8 (7.2-8.5)	194	0.25 (0.20-0.50)	194
1		12.8 (10.7-13.8)	21	0.80 (0.24-1.00)	21
2		14.6 (13.3-15.7)	17	1.85 (1.20-2.20)	17
3	Male	18.2 (17.0-19.5)	3	2.31 (1.85-2.85)	3
	Female	19.5 (18.3-22.1)	7	2.81 (1.90-3.40)	7
4	Male	25.3	1	3.30	1
	Female	31.4 (28.9-33.9)	2	3.70 (3.30-4.10)	2
5	Female	3.50	1	4.25	1
6	Female	3.75	1	4.33	1

beside the female. Captive matings occurred mostly in the morning (08:10–11:15 hrs), but two occurred in the afternoon (04:00 hrs, 04:31 hrs), and two in the early evening (07:19 hrs, 07:50 hrs); no night observations were made. Copulations lasted 19–30 min. Nine of the pairs were found copulating on more than one occasion. Two copulating pairs of *S. dekayi* were found at Edward Hand at 09:31 hrs on 30<sup>th</sup> April 1961 and 08:39 hrs on 5<sup>th</sup> May 1960.

Parturition by the captive females occurred between 20<sup>th</sup> August and 15<sup>th</sup> September after gestation periods of 81–94 days after the first observed copulation. The females fed only sparingly from July until the birth of their young. Wild neonates were found in September at both study sites. The captive females produced a total of 194 neonates (190 alive, 4 stillborn; Table 4). Litter size was 6–19 (mean 12) young. The largest (presumably oldest) females produced the greatest numbers of offspring per litter; females 35 cm or longer had litters of 12–19 young, females shorter than 35 cm produced litters with 6–13 young. Although not significantly different, neonates

Table 4. Length and mass relationships of known age *Storeria dekayi* in Lancaster County, Pennsylvania (1960–1967).

from the larger litters were slightly shorter and weighed slightly less than those from litters containing smaller numbers of offspring. Neonate SVL and mass were not significantly correlated with female size or weight.

#### Growth

SVL and mass were recorded for all captured *S. dekayi*. Moreover, similar data were taken from 194 neonates born in captivity. Data from known age snakes are presented in Table 4. These data are similar to those from Kansas *S. d. texana* (Fitch, 1999), although the Pennsylvania snakes were slightly longer and more massive. Combined adult SVL and mass data compiled at both Lancaster County sites ( $n = 975$ ) were as follows: males, mean SVL 24.2 cm (17.0–27.0 cm), mean mass 4.41 g (1.85–5.50 g); females, mean SVL 28.9 cm (18.2–49.0 cm), mean mass 8.09 g (1.80–16.45 g).

Neonates grew rapidly in the first months after birth, but growth was slower in juveniles, and the growth rate slowed even more in adults. One hundred ninety neonates (four were stillborn) were released within a day of their birth in August. Ten recaptured in September had a mean SVL of 8.9 (8.0–9.4) cm, a mean increase of 14.1%; and a mean mass of 0.33 (0.25–0.40) g, an increase of 32%. Two recaptured in early October had grown to 8.3 cm (0.44 g) and 9.0 cm (0.62 g), respectively. Eleven recaptured year old juveniles had an average increase in SVL of 10.9%, and an increase of 24.5% in mass; and 10 second year recaptured young had grown an average of 8.2% in SVL, and 22.2% in mass.

#### Feeding observations

Observations of foraging behaviour were made at both study sites. All feeding observations took place in the evening or night between 19:35 hrs and 21:02 hrs. The earliest was on 29<sup>th</sup> April, the latest on 15<sup>th</sup> September, a possible annual feeding duration of 140 days in Lancaster County.

Earthworms, the primary prey of *S. dekayi* (Ernst & Ernst, 2003), were abundant at both study sites. Ten of the snakes were seen tracking earthworms, and six others were found ingesting them. The worms were apparently located by their scent. Once the worm's odor trail was found, the snake quickly followed it with much tongue-flicking until the worm was located. The snake at once examined the worm with several tongue flicks, and then bit it along its body. The snake worked along it by alternately releasing its jaws and then biting the worm farther along its body toward the closest end. Once the snake reached the end of the worm, it aligned its mouth and body with that of the worm and began to swallow it. No preference was noted as to which end, head or tail, of the earthworm was swallowed. Swallowing usually began at the closest end of the worm from the initial bite position, only one snake worked to the farthest end before swallowing the worm. Most worms were ingested within three minutes (mean 160 sec). Two other *S. dekayi* were found ingesting small slugs; the swallowing behaviour did not differ from that used to ingest earthworms.

On two occasions, captive female *S. dekayi* ate their newborn young before they could be counted or measured. Ernst & Ernst (2003) present a list of reported prey of *S. dekayi*.

#### Injuries, predation and parasites

The only nonpredatory injuries noted were of four (0.5%) individuals with bobtails, probably caused by frost bite, and another (0.1%) with a jagged abrasion on its side. Only three snakes were found to have been predated: one had been pecked by a bird, another was found with its head chewed off (apparently by a small mammal), and an 10.6 cm SVL individual was regurgitated by a 63 cm SVL Common Garter Snake, *Thamnophis sirtalis*. Several birds, including American Robins (*Turdus migratorius*), which were common at both sites, are known to prey on *S. dekayi* (Ernst & Ernst, 2003). Forty-one *S. dekayi* had mite infestations beneath their scales when first captured in the early spring, but all recaptured later lacked scale mites and had apparently cast them off with the first ecdysis of the year. The rates of predation and mite infestation in the Pennsylvania populations were not high.

#### DISCUSSION

The differences in the lengths of the annual activity period of the two sites may have occurred because the stone wall at Slackwater, the main center of activity there, was almost constantly in shade during the day. At Edward Hand, the trees were more scattered and the canopy cover more open allowing more sunlight to reach the ground and warm it faster than at Slackwater. The annual activity period at the two sites is slightly shorter than the monthly activities of Kansas and North Carolina *S. dekayi* reported by Fitch (1999) and Palmer & Braswell (1995). Fitch (1999) reported an annual activity period of mid-March to mid-November, or about 245 days in Kansas, and Palmer & Braswell (1995) found the snake active in every month in North Carolina, but more so in the spring. Possibly the ground and air temperatures average higher in Kansas and North Carolina than at the two Pennsylvania study sites. As in southeastern Pennsylvania, the annual activity period is bimodal in North Carolina,

where 53% of captures occur between March and June (Palmer & Braswell, 1995).

Snakes at Edward Hand overwintered under debris piles, in rotten logs, or within rodent burrows (one record). At Slackwater, the snakes used cavities in the stone wall and old logs. The hibernacula in the stone wall were entered at ground level, and either extended laterally into the wall 20–25 cm or at a slight downward slope to 20–30 cm.

Lachner (1942) reported a hibernaculum in a Pennsylvania gravel bank, and Bailey (1948) another in an Iowa roadside embankment. Winter mortality by freezing may be high (Bailey, 1948).

Recaptures of the same individuals at a particular hibernaculum over several years indicated a high philopatry (site-fidelity) rate; with mean return rates of 67% (40–83%) at Slackwater, and 63% (55–75%) at Edward Hand. At Slackwater only 12 *S. dekayi* changed hibernacula over the years; at Edward Hand 14 individuals changed hibernation sites from one year to the next. Spring aggregations at hibernacula ranged from 2–13 snakes (mean 5 individuals), and fall aggregations 5–10 snakes (mean 6.7 individuals). At Slackwater, eight *S. dekayi* were found on 20<sup>th</sup> January 1967 in a hole in the rock wall approximately 25 cm long and 4 cm deep. At Edward Hand, six individuals were found on 2 February 1961 within a single rotting log. On both occasions the snakes were coiled together in a ball.

The daily activity cycle of *S. dekayi* at the two southeastern Pennsylvania sites followed the pattern typical of North American colubrid snakes (Ernst & Ernst, 2003).

The BTs recorded from Pennsylvania snakes closely match other reported BTs, although the highest BT in Pennsylvania is slightly greater. Clarke (1958) recorded BTs of 2–27°C for *S. dekayi* in Kansas, and Brattstrom (1965) and Fitch (1999) reported BTs of 20.4–27.0°C at ATs of 12.8–28.0°C.

Soil temperatures vary less than air temperatures, and the BTs of both active ( $n = 725$ )



Northern Brown Snake (*Storeria dekayi*). Photograph © Carl Ernst.

and hibernating ( $n = 90$ ) Pennsylvania *S. dekayi* most closely matched the ST than AT (Table 3).

Based on a calculation of mean population size using four different methods, an Ontario population of *S. dekayi* consisted of 545 snakes (96–1,160 individuals) (Freedman & Catling, 1978). Fitch (1999) reported an estimated density of 42 snakes/ha in an open Kansas woodland, and Freedman & Catling (1978) reported one of 70 snakes/ha in the habitat most occupied at an Ontario site. Apparently, sites with more cover objects can support larger populations of *S. dekayi*, as was seen at the Edward Hand site. The adult sex ratio at the Ontario site studied by Freedman & Catling (1978) was 0.36:1.00, slightly lower than those at the two Pennsylvania sites. The mean population sizes, densities, adult sex ratios, and juvenile to adult ratios of the two Pennsylvania sites showed them to be viable populations during the period they were studied. Unfortunately, both sites have been developed into home sites since the 1960s, and both populations were consequently extirpated.

Freedman & Catling (1979) reported the average home range of *S. dekayi* in an Ontario, Canada population was shorter than 60 m, so those calculated for *S. dekayi* at the two Pennsylvania sites are not out of line. Snake home range dimensions essentially become larger with an increase in SVL of the species (Ernst & Ernst,



2003), and a short snake such as *S. dekayi* would be expected to have a relatively small home range, as indicated in this study. Nevertheless, some *S. dekayi* made relatively long movements over time (> 600 m) for their size. Even greater movements have been reported. Noble & Clausen (1936) recorded movements up to 1.2 km by marked *S. dekayi*, and migrations from summer feeding ranges to upland hibernacula are made by some populations of *S. dekayi* (Towey & Tucker, 2001).

Courtship and mating in wild *S. d. dekayi* occurs as early as February and March and continues through May (Clausen, 1936). Copulations by captive and wild Pennsylvania individuals also occurred within this period. Noble (1937) published a detailed description of courtship behaviour in *S. dekayi*, and courtship observations on captives in Pennsylvania showed they followed a similar pattern. Ovulation usually occurs in late March or April, but may take place as late as July in Louisiana (Kofron, 1979). Four dissected Edward Hand females had ovulated in May, later than in Louisiana females. This is best explained by the difference in latitude, and, probably, a longer annual activity period in Louisiana.

Noticeably pregnant females were found at both Lancaster County sites in June and July, and, based on captive birth dates, parturition probably occurred in late August or early September. Known captive gestation periods ranged from 81–94 days, well within the 14–113 day periods reported by Clausen (1936), King (1997), Kofron (1979), and Velhagen & Savitsky (1998).

Literature records of litter size in *S. dekayi* are 3–41 young (Morris, 1974; Wright & Wright, 1957), and the 6–19 neonates/litter produced by the captive Pennsylvania females fall within this range. Although, data on the relationship of neonate size and mass to female size showed that female size possibly influences both neonate size, litter size was dependent on female size. This supports the optimal egg size model, which states that variation in reproductive output will be in clutch (= litter) size, not in egg (= offspring) size (Smith & Fretwell, 1974). The relative clutch mass (RCM) calculated using the female's postpartum body mass averaged 0.40 (0.32–0.43); this agrees favourably with the 0.36–0.48 RCMs reported for the species (Meshaka, 1994; Seigel & Fitch, 1984).

Male *S. dekayi* mature at a SVL of 15–16 cm (Fitch, 1999; King, 1997; Mitchell, 1994), and females mature between 17.0–17.5 cm SVL (Kofron, 1979; Mitchell, 1994); both sexes mature in 2–3 years. Once the snake's sex could be determined at three years from its tail length, Pennsylvania females were always longer and heavier than males (Table 4). Data from recaptured juveniles showed that they grew at an annual SVL rate of 8–11%. The annual SVL growth rate of recaptured adult males was 4.2%, and that of adult females, 6.0%. The growth rate decreases with age, as in other North American snakes (Ernst & Ernst, 2003). The oldest known recaptured *S. dekayi*, a female at Edward Hand, was in her sixth year (Table 4). The record longevity for the species is 7 years, 13 days in captivity (Snider & Bowler, 1992).

Observed feedings by wild and captive Pennsylvania *S. dekayi* indicated that the feeding periods coincided with the snakes' daily activity times. The annual feeding period of 140 days was probably determined by the environmental temperatures, and possibly by summer drought conditions which forced many of the snakes underground in 1966. The snakes were not found to feed until the surface temperature had reached 22°C (Table 3). A diet of earthworms and slugs is well known for this species (Ernst & Ernst, 2003), but the ingestion of neonates by females has not been previously reported. Perhaps unknown stresses of captivity triggered this behaviour.

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